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1 **“Does Drought Influence the Relationship between Biodiversity and**
2 **Ecosystem Functioning in Boreal Forests?”**

3

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19 Author contribution:

20 DB, AG¹ and AG² designed the experimental study. DB and CG conducted the field work. TJ

21 provided the productivity data. CG, DB, TJ, AG¹ and AG² analyzed the results. CG and DB

22 wrote the first draft of this manuscript and all authors substantially contributed to revisions.

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33 **Abstract**

34 In mixed forests, interactions among species influence ecosystem functioning but
35 environmental conditions also play an important role in shaping relationships between
36 biodiversity and ecosystem functioning. In the context of climate change, the carbon and
37 water balance in pure vs. mixed forest stands may be differentially influenced by changing
38 soil water availability. To test this hypothesis, we compared the influence of biodiversity on
39 water use efficiency (WUE_s) in boreal forests between wet and dry years. We assessed the
40 carbon isotope composition ($\delta^{13}\text{C}$) of tree rings in *Betula pendula*, *Pinus sylvestris* and *Picea*
41 *abies* growing in pure vs. mixed stands. In addition, we tested whether differences in WUE_s
42 affected patterns of basal area increment (BAI_s). No biodiversity effect was found for stand
43 $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_s$) during the wet year. However, there was a significant increase in $\delta^{13}\text{C}_s$ between
44 the wet and the dry year and a significant effect of biodiversity on $\delta^{13}\text{C}_s$ in the dry year. The
45 increase in $\delta^{13}\text{C}_s$ in mixed stands was associated with both selection and complementarity
46 effects. Although BAI_s decreased significantly in the dry year, changes in $\delta^{13}\text{C}_s$ did not
47 translate into variations in BAI_s along the biodiversity gradient. Our results confirmed that the
48 physiological response of boreal forest ecosystems to changing soil water conditions is
49 influenced by species interactions and that during dry growing seasons, species interactions in
50 mixed stands can lead to lower soil moisture availability. This illustrates that biodiversity
51 effects can also be negative in mixed stands in the sense that soil resources can be more
52 intensively exhausted. Overall, our results confirm that in boreal forests, the biodiversity-
53 ecosystem functioning relationship depends on local environmental conditions.

54 **Key-words:** biodiversity, boreal forest, drought, $\delta^{13}\text{C}$, mixed forest, water use efficiency

55 INTRODUCTION

56 The biodiversity and ecosystem functioning (B-EF) relationship has received growing interest
57 from ecologists throughout the last two decades due to the rapid loss of diversity observed
58 during the last century (Symstad and others 2003). Several mechanisms have been put
59 forward to explain how community composition and richness can either negatively or
60 positively influence ecosystem functions. A negative influence on biodiversity can result from
61 direct competition for resources among species in a given ecosystem. Negative interactions
62 commonly arise when ecological niches overlap and/or when species share the same
63 functional characteristics and are thus functionally redundant in the ecosystem (Naeem 2008;
64 Vilà and Sardans 1999). In contrast, positive B-EF relationships are commonly attributed to
65 two other mechanisms: complementarity and selection. Complementary use of resources
66 among species refers both to ecological niche partitioning and facilitation (Loreau and Hector
67 2001) and implies species coexistence without major interspecific competition for resources.
68 The selection effect recognises that the probability of occurrence of high-performing species
69 is greater in highly diverse ecosystems (Loreau and Hector 2001). Studies investigating
70 complementarity and selection effects mainly focused on ecosystem productivity (e.g.
71 Bradford 2011; Fargione and others 2007; Isbell and others 2009; Morin and others 2011;
72 Zhang and others 2012), while only a few were interested in other ecosystem functional traits
73 (e.g. Forrester and others 2010; Kunert and others 2012; Meinen and others 2009).

74 In addition to competition, complementarity and selection effects, local environmental
75 conditions also play an important role in shaping B-EF relationships (Belote and others 2011;
76 Hooper and Dukes, 2004). Under the assumptions of the “stress-gradient” hypothesis, which
77 predicts that the net outcome of biotic interactions (competition and facilitation) shifts from
78 negative to positive along gradients of limiting physical conditions (Bertness and Callaway
79 1994), positive biodiversity effects are expected to be more common in severely resource-

80 limited conditions while negative effects should prevail in richer and milder environments.
81 This general conceptual model has recently been refined (Maestre and others 2009) and is
82 widely supported in the literature (Herbert and others 2004; Jucker and Coomes 2012; Steudel
83 and others 2012; He and others 2013; Wang and others 2013). In the context of climatic
84 change, most regions around the world are expected to encounter more extreme
85 environmental conditions (IPCC, 2007). The “stress-gradient” hypothesis is therefore of great
86 interest since B-EF relationships are likely to change in the future. Whether or not more
87 diverse ecosystems might be better adapted and/or more resilient to these changes is an
88 important issue to investigate.

89 In the boreal climate zone, simulations predict a general shift from short, cool summers
90 towards longer, warmer summers (IPCC 2007; Jylhä and others 2010). Thus, boreal forest
91 ecosystems are expected to encounter more frequent and intense reduced soil water
92 availability in summer. Contrasted responses of carbon and water fluxes in forest ecosystems
93 to warmer and drier climate have already been observed (reviewed in Boisvenue and Running
94 2006). Few studies so far were conducted on the response of boreal forests to these
95 conditions. Nevertheless, Dulamsuren and others (2010) showed that increasing summer
96 temperatures accompanied by decreasing precipitation lead to reduced productivity in taiga
97 forests in Mongolia.

98 Plants adapt to reduced soil water conditions through numerous physiological and/or
99 morphological processes (review in Kozłowski and Pallardy 2002). At the leaf level, under
100 drought conditions, they must manage the trade-off between optimum carbon gain for growth
101 and loss of water through transpiration (Farquhar and others 1982) which usually results in an
102 increase in intrinsic water use efficiency (WUE_{int}), defined as the ratio between CO_2
103 assimilation during photosynthesis and stomatal conductance for water vapour (e.g. Zhang
104 and Marshall 1994). At ecosystem level, carbon and water fluxes are influenced by species-

105 specific functional responses to environmental conditions and by intra- and inter-specific
106 interactions both below- and above-ground. Both positive and negative interactions among
107 species may occur in mixed stands and this may lead to differing spatial and temporal
108 resource availability and physiological and morphological adaptations within species. These
109 complex interactions mean that general predictions on stand-level water use efficiency
110 (WUE_s) under dry conditions cannot solely be based on individual species responses to these
111 conditions.

112 In this context, little information is available concerning the relationship between tree
113 biodiversity and the regulation of carbon and water fluxes in boreal forest ecosystems.
114 Gamfeldt and others (2013) found positive relationships between tree species richness and
115 multiple ecosystem services (tree biomass, soil carbon storage, berry production and game
116 production potential) in production forests in Sweden and explained the observed positive B-
117 EF relationship by facilitation processes among tree species. In contrast, Grossiord and others
118 (2013a) found no complementary effect for biomass production and WUE_s in a young boreal
119 plantation, though they did find a weak selection effect. These studies, however, did not
120 compare the B-EF relationship in contrasted environmental conditions.

121 In this study, we tested the following assumptions: i) in boreal forest ecosystems, the stand-
122 level carbon and water balance under non-limiting soil water conditions (wet year) should not
123 necessarily depend on biodiversity effects, and ii) under limiting soil water conditions (dry
124 year), species identity, species combinations and richness levels should influence ecosystem
125 functioning. We analyzed the influence of species richness on time-integrated WUE_s
126 estimated from the carbon isotope composition ($\delta^{13}C$) (Farquhar and others 1982) of ring
127 whole wood measured in tree rings from two years with contrasting soil water conditions (wet
128 year in 2004 and dry year in 2006). Samples were taken from 26 mature stands in Eastern
129 Finland, which were either pure or mixed with varying percentages of *Betula pendula*, *Pinus*

130 *sylvestris* and *Picea abies*. We also tested whether changes in WUE_s would influence stand
131 basal area increment (BAI_s).

132

133

134 MATERIALS AND METHODS

135 Site description

136 The study was conducted in August 2012 in 26 stands of boreal forest that are distributed over
137 a 2000 km² area around Joensuu, Finland (62.60°N, 29.76°E). The stands were 30 m x 30 m
138 and included pure, 2-species mixture, or 3-species mixture of Scots pine (*Pinus sylvestris*),
139 Norway spruce (*Picea abies*) and Silver birch (*Betula pendula*). Four replicates of each
140 combination were selected except for pure birch stands that were sampled only twice. Mean
141 tree age within the stands was 33.9 ± 5.8 years. Tree species characteristics are given in Table
142 1.

143 The stands were selected according to the following specifications: no change in management
144 had occurred in the last 5 years; confounding factors like altitude, topography or soil type
145 were kept to a minimum between selected stands; in a given forest patch, the stands were
146 more than 500 m apart to avoid spatial autocorrelation; stands were mostly even-aged and
147 single-layered. More detailed information on the selection procedure of the study stands can
148 be found at <http://www.fundiveurope.eu>. The selected stands were situated between 80 and
149 200 m a.s.l. on Podzols soils (FAO classification) above mica schist bedrock. Mean annual
150 rainfall in the region is around 700 mm and mean annual temperature is 2.1°C.

151

152 Selection of the target years

153 The daily water balance model “BILJOU” (Granier and others 1999) was implemented in
154 order to quantify soil water availability at a daily time-scale in the study region and then to
155 select the driest and the wettest year over the past fifteen years. We used above-canopy
156 measurements of daily meteorological conditions (rainfall, global radiation, air temperature
157 and humidity, wind speed) from the Hyytiälä forestry field station (61.84°N, 24.28°E, 153 m

158 a.s.l.) to run the model. Although this meteorological station is situated 300 km south-west of
159 Joensuu, it is the nearest source from which data could be obtained to estimate daily relative
160 extractable soil water (REW) over the 1997-2011 period (Fig. 1). The model was initialized
161 assuming that soil was at field capacity on 1st January. We used a leaf area index of 5.0 m² m⁻²
162 and a soil holding capacity of 125 mm as input data for model simulations. We discarded the
163 years 1998 and 2010 because of too many missing data. Soil water deficit was assumed to
164 occur when the REW dropped below 0.4, a threshold value that has been shown to induce
165 stomatal closure and interrupt radial growth in forest trees (Granier and others 1999). For each
166 remaining year from 1997 to 2011, we characterized annual water stress using the starting day
167 and the duration of the period when REW dropped below the threshold limit coupled with a
168 water stress index which cumulates the difference between simulated REW and the 0.4
169 threshold (Granier and others 1999). These calculations revealed that in 2006 water stress was
170 the most severe and in 2004 it was the least severe (Fig. 1). Drought started on June 16 in
171 2006 while there was no drought in 2004. Total precipitation during the growing season (May
172 to September) was 157 and 303 mm in 2006 and 2004, respectively.

173

174 **Wood carbon isotope composition**

175 Six trees per species in each pure stand and three trees per species in mixed stands were
176 randomly selected among the ten trees with the largest diameter at breast height. For each
177 selected tree we extracted one 5-mm-diameter wood core at breast height (1.3 m) from the
178 south side of the trunk. The fresh samples were shipped to INRA Nancy and oven-dried at
179 50°C for 72 hours to reach constant weight before being filed with a scalpel for tree-ring
180 dating. For both target years, we carefully extracted the late wood with a scalpel. The wood
181 fragments from a given species in a given stand were then pooled and ground into a fine
182 powder. We combined the wood fragments from individuals of the same species in the same

183 stand to obtain enough material for carbon isotope analyses, to ensure adequate sample
184 homogeneity, and to reduce experimentation costs. Although we sampled only a few trees per
185 species in each stand, the level of replication was adequate given the imprint of environmental
186 signals on tree-ring carbon isotope composition (e.g. Peñuelas and other 2008). From 0.4 to
187 1.5 mg of the ground wood samples were weighed on a high-precision scale (MX5, Mettler
188 Toledo, Viroflay, FR) and placed into tin capsules (Elemental Microanalysis Limited, Devon,
189 UK) for $\delta^{13}\text{C}$ analyses. Samples were analyzed with a PDZ Europa 20-20 isotope ratio mass
190 spectrometer (Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility of UC Davis, CA,
191 USA. All isotopic measurements are reported in the standard delta notation (δ , ‰):

$$192 \quad \delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad [1]$$

193 where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios of the samples and the Vienna Pee Dee
194 Belemnite (VPDB) standard.

195

196 **Wood basal area increment**

197 To quantify productivity, we randomly selected five trees per species from each pure stand,
198 and three trees per species in mixed stands, among the twelve (pure stands) or eight (mixed
199 stands) trees with the largest diameter at breast height. For each tree, one 5-mm-diameter
200 wood core was extracted at breast height from the south side of the trunk. These cores were
201 different from the ones taken for $\delta^{13}\text{C}$ analysis. Once air dried, the core samples were mounted
202 on wooden boards and then sanded with paper of progressively finer grit sizes. A high
203 resolution (2400 dpi) flatbed scanner was then used to image the cores, following which
204 diameter growth measurements and crossdating were performed with the CDendro software
205 suite (Cybis Elektronik & Data, Saltsjöbaden, Sweden). For each of the studied years,
206 diameter growth measurements of the individual trees were converted to basal area increment,

207 then standardized basal area increment (BAI_i , $\text{cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$) was obtained by dividing basal
208 area increment by the basal area of each tree.

209

210 **Stand-level carbon isotope composition and basal area increment**

211 Based on species-specific $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_i$) for each stand, we calculated stand-level carbon
212 isotope composition ($\delta^{13}\text{C}_s$). The contribution of a given species to $\delta^{13}\text{C}_s$ depends on its
213 species-specific contribution to stand CO_2 assimilation rates (Lloyd and Farquhar 1994).
214 Consequently, when $\delta^{13}\text{C}_i$ values are scaled up from species level to stand level, $\delta^{13}\text{C}_i$ values
215 should be weighted by species assimilation rates. However, since species-specific CO_2
216 assimilation rates were not available in this study, we used species total basal area (BA_i , cm^2)
217 in each stand as a proxy, following Bonal and others (2000). $\delta^{13}\text{C}_s$ was thus calculated as:

$$218 \quad \delta^{13}\text{C}_s = \frac{\sum_{i=1}^N BA_i \delta^{13}\text{C}_i}{\sum_{i=1}^N BA_i} \quad [2]$$

219 where N is the number of species in the mixture.

220 $\delta^{13}\text{C}$ in C_3 plants constitutes a record of the intercellular / atmospheric CO_2 concentration ratio
221 during the period in which the carbon was fixed and is strongly positively correlated to leaf
222 intrinsic water use efficiency (WUE_{int}) (Farquhar and others 1982) as shown in the following
223 equation:

$$224 \quad \delta^{13}\text{C}_s = \frac{a}{b} \ln \left(\frac{C_a}{C_i} \right) + \delta_a \quad [3]$$

225 where C_a is the CO_2 concentration in the atmosphere, δ_a and $\delta^{13}\text{C}$ are respectively the carbon
226 isotope compositions of the atmosphere and of the sample, a represents the fractionation
227 occurring due to diffusion in air (4.4 ‰), and b is the fractionation caused by carboxylation
228 (27 ‰). We thus used Equation 3 to calculate stand-level water use efficiency (WUE_s) based
229 on $\delta^{13}\text{C}_s$.

230 To estimate stand basal area increment (BAI_s , $\text{cm}^2 \text{cm}^{-2} \text{yr}^{-1}$) of the two studied years (2004
231 and 2006) and of the year following the driest year (2007), we considered the relative
232 importance of each species in terms of contribution to total basal area. Thus, BAI_s was
233 calculated as:

234
$$BAI_s = \sum_{i=1}^n p_i \cdot BAI_i$$
 [4]

235

236 **Data analysis**

237 All analyses were performed using the statistical software R 2.14.1 (R Development Core
238 Team, 2011). We tested three effects that could impact $\delta^{13}\text{C}_i$, $\delta^{13}\text{C}_s$, BAI_i and BAI_s . Firstly, tree
239 biodiversity, which we characterised for each stand with the Shannon biodiversity index. This
240 index expresses the uncertainty of predicting the proportion of stand basal area a given tree
241 species represents in binary digits (ranging from zero for pure stands to the logarithm in base
242 two of the total basal area of the species in the stand). Secondly, competition intensity in each
243 stand, which we expressed as the total basal area of the stand. Thirdly, year. We applied a
244 series of mixed-effect models to analyze the impact of the three effects and their interactions
245 on $\delta^{13}\text{C}_i$, $\delta^{13}\text{C}_s$, BAI_i and BAI_s with “stand” as a random effect. To test for any biodiversity
246 effect during the recovery phase to drought (year 2007), we applied the same mixed-effect
247 model on BAI_s . Contrasts were used to test for relevant differences between fixed effects
248 when the overall model was significant. We calculated the difference in $\delta^{13}\text{C}_s$ and BAI_s
249 between the dry and wet year ($\Delta\delta^{13}\text{C}_s$ and ΔBAI_s , respectively) and used Spearman
250 regressions to test the relationship between the Shannon biodiversity index and $\Delta\delta^{13}\text{C}_s$ or
251 ΔBAI_s .

252 When a significant effect of biodiversity on $\delta^{13}\text{C}_s$ or BAI_s was observed, we evaluated the net
253 biodiversity effect, the complementarity effect, and the selection effect on $\delta^{13}\text{C}_s$ or BAI_s with

254 the method developed by Grossiord and others (2013b). We used one-way ANOVA and post-
255 hoc Tukey tests to check for differences in these biodiversity effects among species richness
256 levels. We used t-tests to check all three biodiversity effects for differences from 0 for each
257 mixture level and for each mixture type (identity of the mixture).

258 RESULTS

259 Wood carbon isotope composition

260 We observed considerable variability in $\delta^{13}\text{C}_i$ across species, species mixtures and years,
261 ranging from -28.7 ‰ for birch in a 2-species mixture with spruce to -26.2 ‰ for spruce in a
262 2-species mixture with pine during the wet year, and from -27.4 ‰ for birch in a mixture with
263 spruce to -24.2 ‰ for pine in a 3-species mixture during the dry year. Mixed-effect models
264 revealed a significant species effect ($P < 0.001$), year effect ($P < 0.001$) and an interaction
265 between Shannon index and year ($P = 0.019$), but no effect of the Shannon index alone, the
266 interactions of the Shannon index and the species, or the interactions of the year and the
267 species ($P > 0.050$). The significant effect of the interaction between Shannon index and year
268 was only observed for pine and spruce ($P = 0.012$ and $P = 0.020$, respectively), indicating for
269 these species a differential response of $\delta^{13}\text{C}_i$ to the mixture in the two years.

270 For each species, whatever the richness level, we found significantly higher values of $\delta^{13}\text{C}_i$
271 during the dry year than during the wet year ($P = 0.003$ for birch, $P = 0.017$ for pine and $P =$
272 0.037 for spruce). For the wet year, we did not observe any effect of the Shannon index or of
273 competition intensity on $\delta^{13}\text{C}_i$ for any species ($P > 0.050$). In contrast, during the dry year,
274 pine and spruce showed a significant positive Shannon index effect ($P = 0.013$ and $P = 0.027$,
275 respectively) and a competition intensity effect ($P < 0.001$ and $P = 0.010$, respectively),
276 whereas birch did not display any significant patterns ($P > 0.050$).

277 At plot level, $\delta^{13}\text{C}_s$ values ranged from -28.1 ‰ for a pine-spruce mixture to -26.6 ‰ for a
278 pure stand of spruce during the wet year and from -26.9 ‰ in a pure stand of pine to -24.6 ‰
279 for a 3-species mixture during the dry year (Fig. 2). We observed a significant effect of year
280 on $\delta^{13}\text{C}_s$ ($P < 0.001$), with higher values of $\delta^{13}\text{C}_s$ during the dry year, as well as a significant
281 interaction between Shannon index and year ($P = 0.012$). Specifically, while there was no

282 significant relationship between the Shannon index or the competition index and $\delta^{13}\text{C}_s$ during
283 the wet year ($P > 0.050$), a highly significant and positive Shannon index effect was apparent
284 ($P = 0.008$) during the dry year, along with a marginal influence of competition intensity ($P =$
285 0.067). Differences in $\delta^{13}\text{C}_s$ between the dry and the wet year ($\Delta\delta^{13}\text{C}_s$) for each stand were
286 positively correlated with the Shannon index ($P = 0.038$).

287

288 **Wood basal area increment**

289 The basal area increment (BAI_i) of individual species ranged from $0.3 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ for
290 pine mixed with birch to $52.9 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ for spruce mixed with pine during the wet
291 year, and from $0.7 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ for pine mixed with birch to $41.7 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ for
292 birch mixed with spruce during the dry year. Mixed-effect models revealed a significant
293 species effect ($P < 0.001$), year effect ($P < 0.001$) and an interaction between the species and
294 the year ($P < 0.001$), but no effect of the Shannon index alone, the interactions between the
295 Shannon index and species, or the interactions between the Shannon index and the year ($P >$
296 0.050). For spruce, we found significantly lower values of BAI_i during the dry year than
297 during the wet year ($P < 0.001$), while for birch and pine, no significant changes in BAI_i were
298 found. For the wet year, we did not observe any effect of the Shannon index or competition
299 intensity on BAI_i for any species ($P > 0.05$). For the dry year, pine showed a significant
300 positive Shannon index effect ($P = 0.035$) and no competition intensity effect ($P = 0.813$).
301 Birch and spruce did not display any significant Shannon or competition effects during the
302 dry year ($P > 0.050$).

303 BAI_s values ranged from $14.9 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ in a birch-pine mixture to $61.3 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2}$
304 yr^{-1} in a pure stand of spruce for the wet year and from $16.9 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ in a birch-pine
305 mixture to $59.8 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ in a birch-spruce mixture for the dry year (Fig. 2). In 2007,

306 the year following the driest year, BAI_s values ranged from $16.8 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ in a pure
307 pine stand to $59.4 \times 10^{-3} \text{ cm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$ in a pine-spruce mixture (Fig. 2). The interaction between
308 the Shannon index and the year was not significant ($P = 0.976$). However, we observed a
309 significant effect of the year on BAI_s ($P = 0.001$), with higher values during the wet year in
310 comparison to the dry and the recovery years (Fig. 2). We did not detect any significant effect
311 of the Shannon index or the competition index on BAI_s in either year ($P > 0.050$). We found
312 that differences in BAI_s between the dry and the wet year (ΔBAI_s) were not correlated with
313 the Shannon index ($P = 0.143$).

314

315 **Biodiversity effects on stand carbon isotope composition**

316 Overall, there was no significant change in either net, complementarity or selection effect on
317 $\delta^{13}C_s$ with increasing species richness during the dry year ($P > 0.050$) (Fig. 3). However,
318 when each mixture level was considered independently, complementarity, selection and net
319 effects were significantly higher than zero in the 2-species mixtures ($P < 0.050$), and mainly
320 positive - although not significantly different from 0 - in the 3-species mixtures ($P > 0.050$).
321 When we tested each different species mixture for significance of the biodiversity effects, we
322 found that none of the three effects were significantly different from zero ($P > 0.050$) in the
323 pine-spruce mixtures. However, for birch-pine and birch-spruce mixtures, net and
324 complementarity effects were significantly higher than zero ($P < 0.050$), while no selection
325 effects emerged ($P > 0.050$).

326 **DISCUSSION**

327 **1. Climate effect**

328 Our stable isotope analysis revealed a strong physiological response in boreal trees to
329 changing soil water conditions and helped clarify the mechanisms responsible for observed
330 changes both at the leaf and stand level. The increase in both individual species' $\delta^{13}\text{C}_i$ and
331 stand level $\delta^{13}\text{C}_s$ from wet to dry years (Fig. 2) reflects an active regulation of carbon and
332 water fluxes in this boreal ecosystem and the strong sensitivity of the three species to limiting
333 soil water conditions. Assuming that the difference in δ_a between the two selected years was
334 negligible, the magnitude of the increase in $\delta^{13}\text{C}_s$ reflected a mean increase in WUE_s of $17.0 \pm$
335 $1.8 \mu\text{mol mol}^{-1}$ (i.e. $+19.2 \pm 1.5 \%$). This increase is consistent with the extensive body of
336 literature documenting the functional response of boreal trees to drought conditions (e.g.
337 Vaganov and others 2009; Zhang and Marshall 1994; Saurer and others 2004). This pattern
338 indicates that in the context of climate change, when more frequent periods of water shortage
339 in north-European regions can be expected (IPCC 2007), the three locally-adapted species
340 studied here will be more efficient in using available water resources for carbon acquisition.
341 However, carbon sequestration and storage rates in wood may well decline; indeed, we found
342 that the increase in stand $\delta^{13}\text{C}_s$ during the dry year was associated with a decrease in BAI_s .
343 This is unsurprising as numerous studies conducted in boreal forests have shown lower
344 productivity under water limiting conditions (e.g. Kljun and others 2007).

345

346 **2. Biodiversity effects under wet conditions**

347 Our results confirmed our first hypothesis that under non-limiting soil water conditions there
348 would be little or no effect of biodiversity on $\delta^{13}\text{C}_s$ and BAI_s (Fig. 2). Interactions among
349 species under non-limiting soil water conditions did not lead to any clear B-EF relationships
350 in our boreal study forests, which is consistent with the expectations of the "stress-gradient"

351 hypothesis (Bertness and Callaway 1994). This result is also consistent with a recent study we
352 conducted over a wet summer on the influence of biodiversity on species- and stand-level
353 carbon and water balance in a young boreal plantation in Finland (Grossiord and others
354 2013a). Therein, we argued that in addition to non-limiting soil water conditions, the young
355 ontogenic stage of the plantation likely caused the absence of any biodiversity effect.
356 However, the present study does not support this assumption. Similar observations made in
357 other ecosystem types also concluded on the absence and/or the decrease of biodiversity
358 effects under non-limiting environmental conditions (e.g. Hughes and Stachowicz 2004;
359 Steudel and others 2012).

360

361 **3. Contrasting biodiversity effects under wet and dry conditions**

362 The major result of this study was the positive relationship between biodiversity and the
363 difference in $\delta^{13}\text{C}_s$ between dry and wet years ($\Delta\delta^{13}\text{C}_s$) (Fig. 2). Drier conditions globally
364 enhanced $\delta^{13}\text{C}_s$, and thus WUE_s , but this influence depended on species interactions. Even
365 though the relationship was rather dispersed, stands with greater diversity showed the greatest
366 increase in $\delta^{13}\text{C}_s$, pointing to a greater compromise between carbon accumulation and water
367 consumption under limiting soil water conditions. However, those changes in ecosystem-scale
368 physiological acclimatization to drought failed to minimize the decrease in BAI_s during the
369 dry year and did not influence the productivity of these plots the following year (Fig. 2). The
370 literature actually mentions this apparent inconsistency (e.g. Vaganov and others 2009). The
371 compromise between carbon acquisition and water loss at leaf or plant level usually has a
372 moderate effect on how much assimilated carbon is invested in secondary growth (Flanagan
373 and Johnsen 1995). Carbon allocation to above- or below-ground components in response to
374 soil water conditions strongly varies among species (e.g. Axelsson and Axelsson 1986) and
375 could partially explain the absence of enhanced BAI_s in our study.

376

377 **4. Origin of the biodiversity effects**

378 Partitioning the influence of biodiversity on $\delta^{13}\text{C}_s$ into selection and complementarity effects
379 revealed that during the dry year the proportionally greater increase in WUE_s observed in the
380 2-species mixtures was a result of both mechanisms (Fig. 3). Selection effects refer to a higher
381 performance of one or several species in mixtures on the cost of others. Therefore, the pattern
382 of increasing $\delta^{13}\text{C}_s$ we observed was most likely driven by the two conifers rather than by
383 birch, since both conifers showed higher $\delta^{13}\text{C}_i$ in 2-species mixtures while birch did not (Table
384 1). Higher $\delta^{13}\text{C}_s$ values in the 2-species mixtures with birch were also partially explained by a
385 complementarity effect, probably as a result of different rooting strategies among the species.
386 Birch is known to have deeper rooting systems that explore larger volumes than those of pine
387 and spruce, thus enabling birch to access both shallow and deep soil layers (Kalliokoski and
388 others 2008). The fact that birch $\delta^{13}\text{C}_i$ values did not respond to increasing diversity during the
389 dry year supports this assumption and suggests that the effects of intra- and inter-specific
390 interactions for water acquisition for this species are similar. In contrast, the complementarity
391 effect for $\delta^{13}\text{C}_s$ was not significant in stands where the two conifers cohabited. *Pinus*
392 *sylvestris* and *Picea abies* are known to present similar rooting system development when
393 cohabiting in mixed stands (Kalliokoski and others 2008). It therefore appears that the two
394 conifers were in part functionally redundant in terms of carbon and water acquisition and use
395 in these mixed stands.

396 Although in the 3-species mixtures none of the three biodiversity effects were significantly
397 different from zero, overall they were generally consistent with results for the 2-species mixed
398 stands (Fig. 3). Numerous B-EF studies have revealed such saturating or even hump-shaped
399 relationships (e.g. Gamfeld and others 2013; Vilà and others 2013). One explanation for this
400 type of pattern is increasing functional redundancy at higher levels of species richness (as

401 observed for the two conifers here), which leads to faster and more complete exploitation of
402 available resources in stands with greater richness.

403

404 **5. Other potential origins of the biodiversity effects**

405 Variations in $\delta^{13}\text{C}$ in tree rings reflect physiological processes of acclimatization to
406 environmental conditions and physical archives of short- or long-term changes in soil
407 moisture and/or air humidity in forests (Saurer and others 2004; Andreu and others 2008;
408 Mölder and others 2011). Therefore, the significantly higher $\delta^{13}\text{C}_s$ values we observed along
409 the diversity gradient in the dry year could be viewed not only as a consequence of species
410 interactions, but also as a result of lower soil water availability in mixed stands as compared
411 to pure ones. High soil moisture exhaustion in mixed stands during dry years was already
412 reported in other hydrological investigations in mixed species forests (Gebauer and others
413 2012). Such a feedback effect could arise because of the particularly high competitiveness of
414 birch for water resources and its high water consumption (Kalliokoski and others 2008). This
415 would lead to a higher drought exposure for the conifers in the mixed stands and thus reduced
416 transpiration through stomatal regulation. This increased drought exposure may have been
417 also the cause for the absence of any increase in BAIs in the mixed stands. Nevertheless,
418 differences in canopy structure inducing different atmospheric humidity and light conditions
419 between pure and mixed stands (Kelty 2006) as well as below-ground competition among
420 these species for nutrients (nitrogen, phosphorus...) may also have contributed to the mixture
421 effects we detected; however, this is beyond the scope of the present study.

422

423

424 **CONCLUSION**

425 In our boreal study region, we demonstrated a clear interaction between the
426 biodiversity/ecosystem carbon and water flux relationship and environmental conditions,
427 consistent with the “stress gradient” hypothesis. The increase in $\delta^{13}\text{C}_s$, and thus in ecosystem-
428 level water use efficiency, with drier soil conditions was much higher in mixed stands than in
429 pure ones, but this did not prevent a decrease in above-ground growth rates with drought. At
430 the species level, functional similarities between the two conifers lead to a redundant
431 contribution of these two species to ecosystem-level carbon and water balance. In contrast, the
432 presence of birch in mixed stands strongly impacted the water use efficiency of the conifers
433 under limiting water conditions. Our results suggest that species interactions in mixed stands
434 during dry growing seasons can lead to lower soil moisture availability as compared to pure
435 ones. This illustrates that biodiversity effects can also be negative in mixed stands in the sense
436 that soil resources can be more intensively exhausted. Our study highlights the need to take
437 into account not only species growth characteristics but also species functional traits when
438 managing boreal mixed forest in order to bolster mixed-forests in a context of climate change.

439

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450

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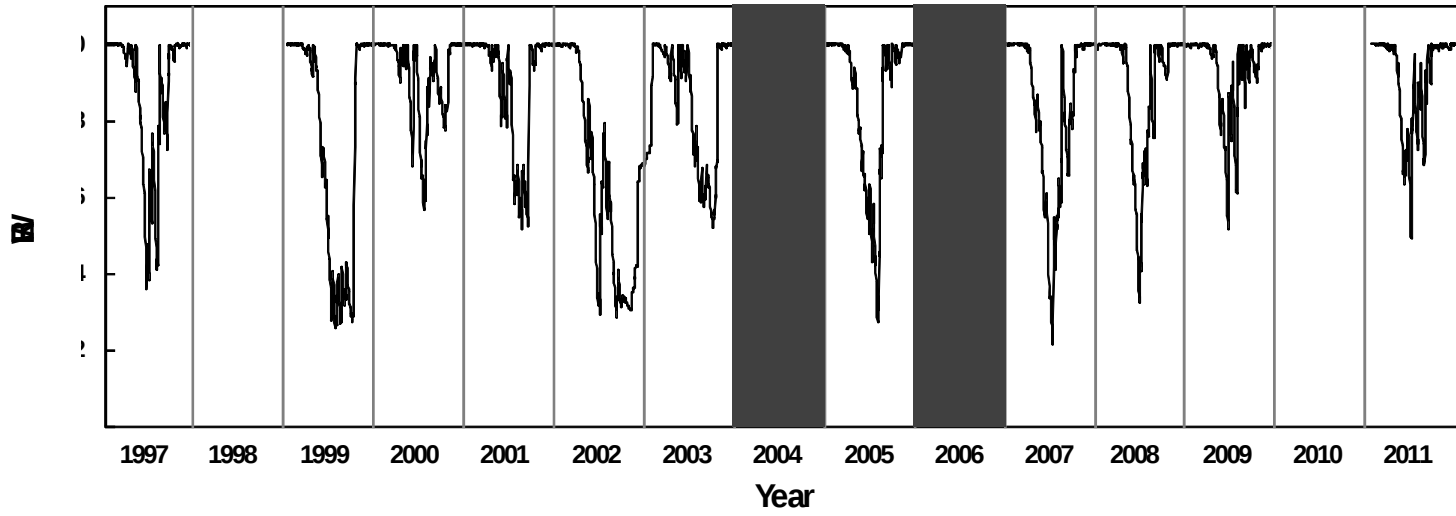
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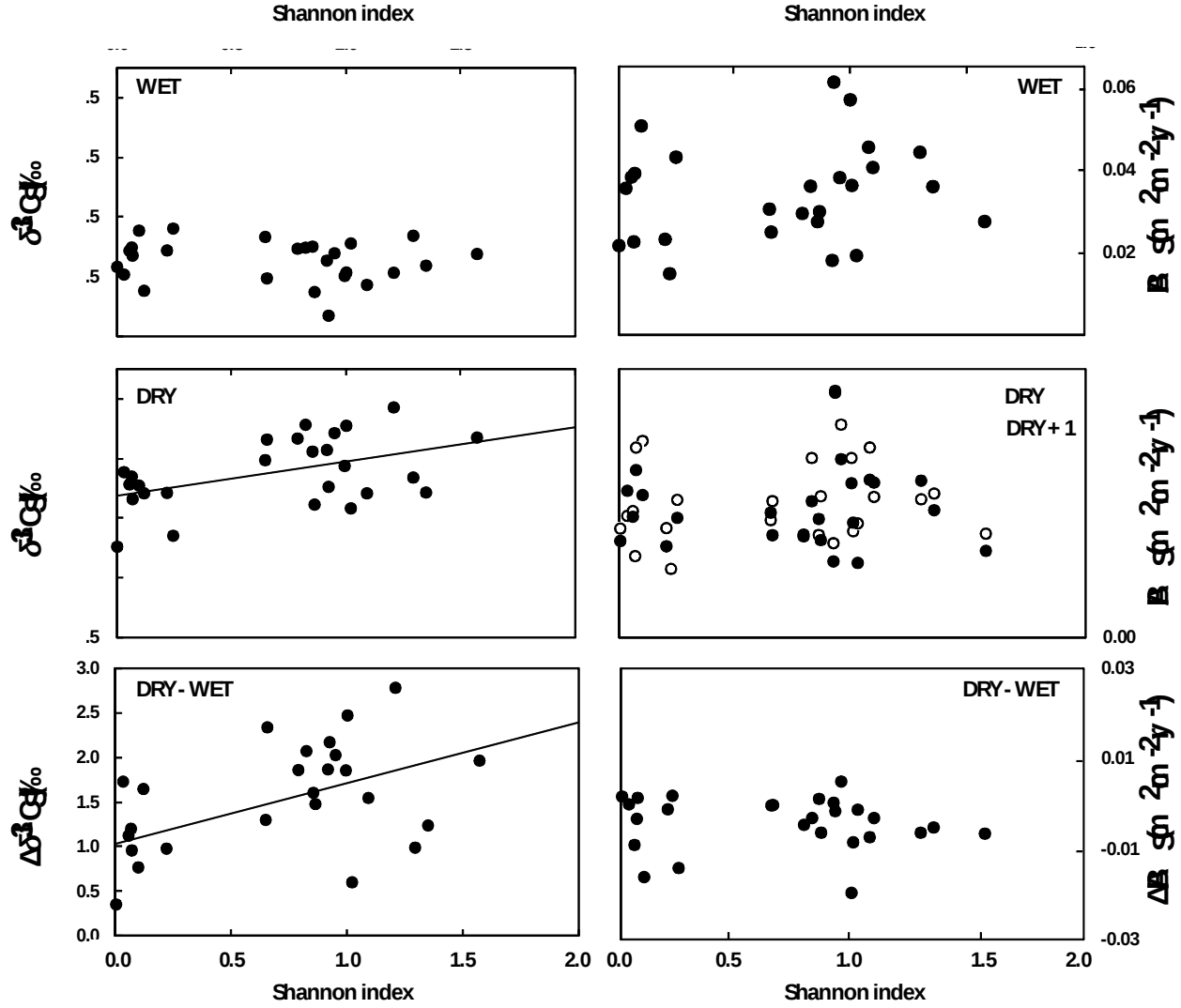
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573

Figure 2

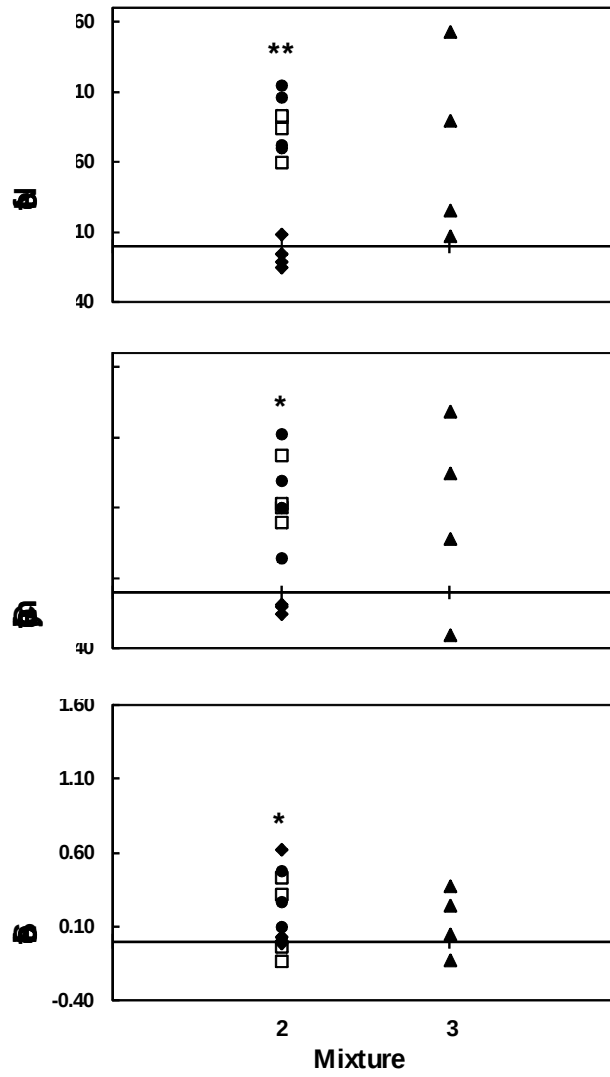


574

575

576

Figure 3



577

578

579 **Figure legends:**

580 **Figure 1:** Time-course of relative extractable water (REW) for the years 1997 to 2012
581 simulated with the “BILJOU” model. The two selected years are highlighted in grey (wet for
582 2004 and dry for 2006).

583

584 **Figure 2:** Stand carbon isotope composition ($\delta^{13}\text{C}_s$, ‰), stand size-standardized basal area
585 increment (BAI_s , $\text{cm}^2 \text{cm}^{-2} \text{yr}^{-1}$) for the wet, the dry and the recovery year (DRY+1, white
586 circles), and the differences in $\delta^{13}\text{C}_s$ and BAI_s between the wet and the dry year ($\Delta\delta^{13}\text{C}_s$ and
587 ΔBAI_s , respectively) as a function of the Shannon biodiversity index. The black lines
588 represent the fitted regression model when the model was significant ($R^2 = 0.22$ and 0.23 for
589 $\delta^{13}\text{C}_s$ and $\Delta\delta^{13}\text{C}_s$, respectively).

590

591 **Figure 3:** Net, complementarity, and selection effects on stand carbon isotope composition
592 ($\delta^{13}\text{C}_s$, ‰) for the dry year as a function of species richness. Black circles indicate birch and
593 pine mixtures, white squares indicate birch and spruce mixtures, black diamonds indicate pine
594 and spruce mixtures, and black triangles indicate 3-species mixtures. Asterisks denote
595 significant differences from zero in the biodiversity effects for each species richness level (t-
596 test, * $P < 0.05$; ** $P < 0.01$).

597

598

599 **Table 1:** Overall mean species diameter at breast height (cm) and mean height (m) with
600 standard errors for *Betula pendula*, *Pinus sylvestris* and *Picea abies*.

601

Species	Mean diameter at breast height (cm)	Mean height (m)
<i>Betula pendula</i>	16.4 ± 0.2	17.9 ± 0.2
<i>Pinus sylvestris</i>	19.2 ± 0.1	17.6 ± 0.1
<i>Picea abies</i>	17.7 ± 0.2	16.1 ± 0.1

602

603

604 **Table 2:** Mean species-specific Shannon biodiversity index, wood carbon isotope
605 composition ($\delta^{13}\text{C}_i$, ‰), and size-standardized basal area increment (BAI_i , $\text{cm}^2 \text{cm}^{-2} \text{yr}^{-1}$) for
606 the dry and wet years, with standard errors for *Betula pendula*, *Pinus sylvestris* and *Picea*
607 *abies*, and for each mixture level.

608

Species	Mixture	Shannon	$\delta^{13}\text{C}_i$ Wet (‰)	$\delta^{13}\text{C}_i$ Dry (‰)	BAI_i Wet ($\text{cm}^2 \text{cm}^{-2} \text{yr}^{-1}$)	BAI_i Dry ($\text{cm}^2 \text{cm}^{-2} \text{yr}^{-1}$)
<i>Betula pendula</i>	1	0.2 ± 0.1	-27.1 ± 0.3	-25.6 ± 0.1	17.1×10 ⁻³ ± 0.8×10 ⁻³	18.2×10 ⁻³ ± 0.9×10 ⁻³
	2	0.9 ± 0.1	-27.8 ± 0.2	-25.8 ± 0.3	19.2×10 ⁻³ ± 0.9×10 ⁻³	19.2×10 ⁻³ ± 0.9×10 ⁻³
	3	1.4 ± 0.1	-27.8 ± 0.2	-25.9 ± 0.5	21.3×10 ⁻³ ± 1.5×10 ⁻³	19.8×10 ⁻³ ± 1.4×10 ⁻³
<i>Pinus sylvestris</i>	1	0.1 ± 0.1	-27.3 ± 0.2	-26.2 ± 0.2	11.9×10 ⁻³ ± 0.7×10 ⁻³	11.4×10 ⁻³ ± 0.7×10 ⁻³
	2	0.9 ± 0.0	-27.2 ± 0.1	-25.7 ± 0.3	16.4×10 ⁻³ ± 0.9×10 ⁻³	15.1×10 ⁻³ ± 0.7×10 ⁻³
	3	1.4 ± 0.1	-26.9 ± 0.2	-25.4 ± 0.6	20.6×10 ⁻³ ± 1.2×10 ⁻³	16.5×10 ⁻³ ± 0.8×10 ⁻³
<i>Picea abies</i>	1	0.1 ± 0.1	-26.9 ± 0.1	-26.2 ± 0.2	22.9×10 ⁻³ ± 1.0×10 ⁻³	17.9×10 ⁻³ ± 0.8×10 ⁻³
	2	0.9 ± 0.0	-27.2 ± 0.2	-25.4 ± 0.3	21.3×10 ⁻³ ± 1.3×10 ⁻³	18.4×10 ⁻³ ± 1.1×10 ⁻³
	3	1.4 ± 0.1	-27.2 ± 0.2	-25.3 ± 0.2	26.6×10 ⁻³ ± 1.5×10 ⁻³	21.9×10 ⁻³ ± 1.3×10 ⁻³

609